

# Invertebrate-Inspired Sensory-Motor Systems and Autonomous, Olfactory-Guided Exploration

FRANK W. GRASSO\*

*Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02453*

**Abstract.** The localization of resources in a natural environment is a multifaceted problem faced by both invertebrate animals and autonomous robots. At a first approximation, locomotion through natural environments must be guided by reliable sensory information. But natural environments can be unpredictable, so from time to time, information from any one sensory modality is likely to become temporarily unreliable. Fortunately, compensating mechanisms ensure that such signals are replaced or disambiguated by information from more reliable modalities. For invertebrates and robots to rely primarily on chemical senses has advantages and pitfalls, and these are discussed. The role of turbulence, which makes tracking a single odor to its source a complex problem, is contrasted with the high-fidelity identification of stimulus quality by the invertebrate chemoreceptor and by artificial sensors.

## Chemical Senses in the Resource Localization Problem

The ability of an animal or an autonomous robot to secure resources (*e.g.*, a supply of energy, a source of water, a shelter from dangerous weather conditions or other hazards) is critical to its behavior and survival. In natural environments critical resources are rarely stable for long. As they are depleted, become inaccessible, or simply disappear, the problem of securing resources is one that autonomous

agents must solve repeatedly. Whether all of the resources in a given region are mapped at once for future use or new resources are found sequentially by foraging as identified ones expire, the activity is exploration.

The first step in exploring for spatially distributed resources is localizing them with appropriate sensory equipment. That animals and robots rely on their senses to locate resources is a tautology: an entity without sensors cannot determine the location of anything. Simple, single-modality search mechanisms have been well studied in robots and invertebrates. If the resource is obvious and detectable from a unique cue, a simple scan with a ranged (distance) sensor from a single site will suffice to locate it. If the resource, and therefore the diagnostic cue, is hidden, a systematic probe of each location in the search region may be required. In the former case no locomotion is required of the animal or robot to localize the resource; in the latter the animal or robot must locomote everywhere. Robots and animals typically employ mechanisms that combine or lie between these two extremes, depending on the complexity of the sensory task.

Optical illusions are the result of a deceived visual sense (Gibson, 1982). Echoes from the substrate can confound auditory localization senses (Mountain and Hubbard, 2001; Robert, 2001). Though the mixing of odors from different sources may muddle olfactory recognition under some conditions, olfaction offers an advantage over vision and audition in sensing the nature of distant objects. By definition, a chemical sensor is detecting a sample that was a physical constituent of the resource. Once detected, therefore, the resource must certainly be in the vicinity, and the agent may then make inferences about the resource's quality. Thus, the chemical senses are advantageous when used in resource localization, because the rate of false positives is low.

Although invertebrates are much more effective than existing robots in chemical tracking, scientists and engineers face three formidable and interrelated challenges that

\* Current address: Dept. of Psychology, Brooklyn College, CUNY, 2900 Bedford Ave., Brooklyn, NY 11210.

E-mail: fgrasso@biomimetics.mbl.edu

This paper was originally presented at a workshop titled *Invertebrate Sensory Information Processing: Implications for Biologically Inspired Autonomous Systems*. The workshop, which was held at the J. Erik Jonsson Center for the National Academy of Sciences, Woods Hole, Massachusetts, from 15–17 April 2000, was sponsored by the Center for Advanced Studies in the Space Life Sciences at the Marine Biological Laboratory, and funded by the National Aeronautics and Space Administration under Cooperative Agreement NCC 2-896.

must be surmounted before invertebrate solutions can be put to work for us in autonomous systems designed for exploration. First, we must thoroughly understand the sensory and behavioral repertoires of organisms that are proficient chemical trackers. Second, we must be able to transfer the principles abstracted from animals to implementation in autonomous systems. The principal pitfall, however, is turbulence, which governs spatial distributions of chemicals in most macroscopic environments. In this essay I discuss the advantages and the pitfalls of identifying the chemical sensing strategies employed in or inspired by invertebrate systems and using them to solve the resource localization problem. Natural fluid-dispersal processes are a two-edged sword: turbulence complicates the chemical tracking problem, but turbulence simultaneously provides a "dynamic similarity" that is invariant in its characteristics across environments.

### The Physics of Tracking Chemicals to Their Source

Tracking an odor (a chemical or chemical cocktail perceived by an olfactory system) to its source might, naively, be imagined to involve the maintenance of the chemical sensors in continuous contact with the odor. The analogy to keeping the image of a visually tracked object fixated on the retina or the vibrations arising from an acoustically tracked object on the cochlea is tempting. However, given that the odor track can be stationary on a solid substrate or moving in the fluid medium above, the olfactory counterpart of the analogy is trail following, not plume tracking.

Among invertebrates, chemical trails are used by conspecifics for social purposes but also by predators or parasites to exploit the trail-leaving individual; and these are distinct behaviors demanding distinct strategies. Ants, for example, follow the pheromone trails left on the substrate by their nest mates (Wilson, 1962). Male snakes locate potential mates by following the chemical signatures left on the ground by females (Ford and Low, 1984; Ford, 1986). Snails (Wells and Buckley, 1972) track similarly, though they sometimes vary their search for mates by indulging in cannibalistic predation (Snyder and Snyder, 1971). Notwithstanding that the strategies underlying these activities are widely recognized for their effectiveness in autonomous systems, they may be of limited utility for exploration of an unknown chemical landscape. In all of these examples—and in the case of cooperative foraging by eusocial insects—salient trails are deliberately generated by one individual for another to follow. Therefore, localization strategies that draw on examples from foraging or hunting creatures hold more promise for autonomous exploration. Shrimp track the odor trail left in the wake of sinking pieces of food (Hamner and Hamner, 1977). For small organisms like bacteria (Alder, 1969) and copepods (Yen, 2000), which operate at spatial scales dominated by diffusion

(rather than turbulent dispersal), odor forms a single, stationary patch contiguous with the source that these creatures exploit. Similarly, nematodes (*Caenorhabditis elegans*) may track the gradients of particles between sand grains to locate mates and sources of nourishment (Morse *et al.*, 1998; Pierce-Shimomura *et al.*, 1999). In any event, however, following a stationary odor trail is only a small part of the behavioral invertebrate repertoire.

Although tracking a stationary odor source may appear to be an easier task than tracking a moving one, the principles of fluid mechanics, upon which olfaction depends, make the problem of the moving trail more tractable. When a stationary object or resource donates portions of itself to the ambient medium through the release of volatile compounds or through surface erosion, that region of space containing the detached chemical from the source is termed a plume (Fig. 1).

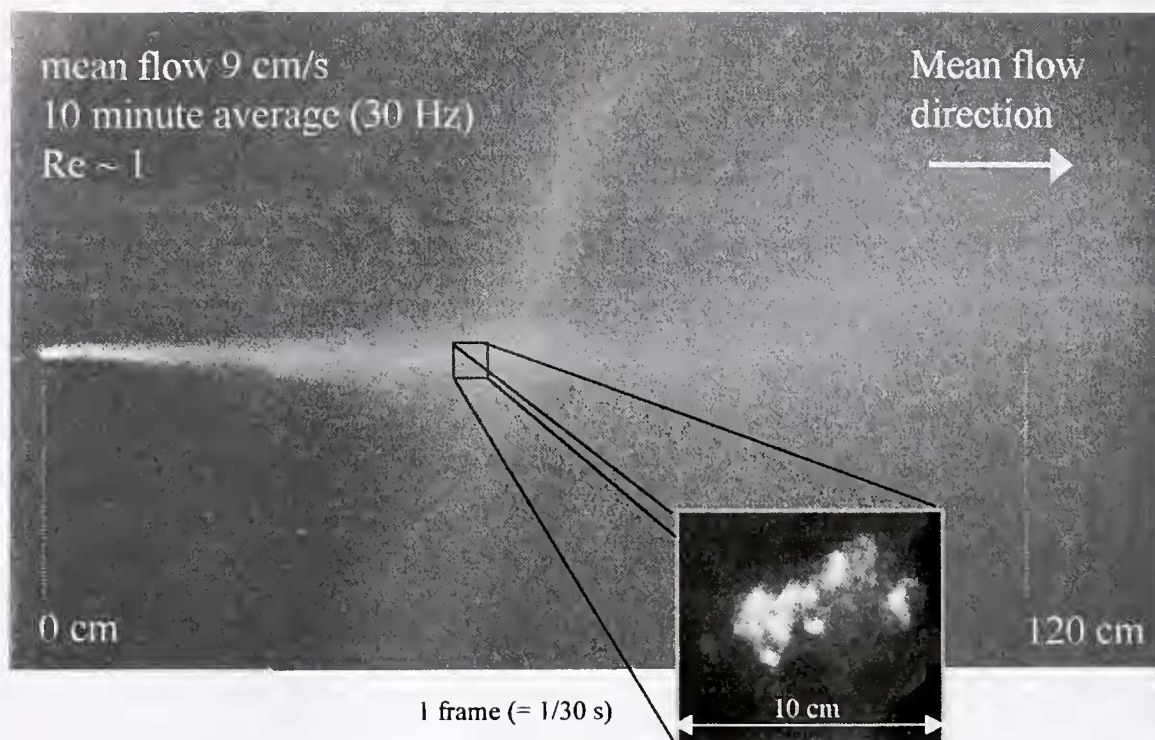
Long-lasting odor plumes from a stationary source can leave traces that accumulate on the substrate. This precipitated odor creates onto the substrate a two-dimensional imprint resembling a time-average image of the plume (Fig. 1). Depending on the conditions, the image might resemble a trail or an annulus, with its highest concentrations near the source. Production of such an image would require stable release and environmental conditions for long periods relative to the dispersal process. Above the micro-scale of nematodes mentioned earlier, no studies of animals tracking such plume images appear in the literature. This is probably because conditions to permit such precipitated plume images are rarely realized physically in natural environments (terrestrial aquatic or marine). This method of inferring a plume from long-term time averages could find application in exploration for persistent resources under conditions favorable to such long-term deposition such as in the vicinity of deep-sea vents or in subterranean caverns.

Most animals that used chemo-orientation to locate resources do so by making use of plumes borne on the fluid medium rather than deposited on the substrate. Among invertebrates, plume tracking is a common olfactory-guided behavior. Because it depends on transport by a fluid, it is fundamentally different from acoustic tracking, visual tracking, or stationary trail-following. For an agent to locate sources of odor, the odor must be carried by the ambient fluid from the surface of the object to the surface of the chemical sensors of the robot or the animal.

The extent to which the continuity of the odor plume is maintained depends on the viscosity of the fluid ( $\nu$ ), the velocity of the fluid ( $U$ ), and the length scale of interest ( $l$ ). The relationship is summarized in the Reynolds number,  $Re$ :

$$Re = lU/\nu$$

When the value of  $Re < 1$  viscous forces dominate, and the continuity of the odor in space will be preserved. This is the regime to which bacteria, copepods, and nematodes are



**Figure 1.** “Leaky” plume characterization in the laboratory. This plume models the odor from an immobile object on the bottom. It was generated in a flume that produced approximately laminar flow. The source, a narrow tube on the floor of the flume, released dye at an “isokinetic” rate matched to that of the ambient flow. We refer to such plumes as leaky to contrast them with jet plumes and wakes that add momentum coincident with the injection of tracer. This is thus a good model for a passive resource on the substrate of a fluid environment. This figure illustrates the spatial distribution of this plume as visualized from trace dye concentration averaged over 5 min at 30 Hz. It shows the plume as a very slow moving animal would experience it with its olfactory organs. This is contrasted with an inset instantaneous ( $<10 \mu\text{s}$ ) section of the same plume as visualized with the laser-induced fluorescence (LIF) method (see text). The inset gives an indication of the intermittent nature of this plume as faster moving animals might experience it.

adapted. At  $Re > 1$  inertial forces dominate, and plume coherence begins to break down. The higher the value of  $Re$ , the greater the degree of turbulence. Most resource localization problems solved by macroscopic invertebrates and those that are of interest for human-scale exploration fall within fluid mechanical regimes that exceed  $Re > 10$ .

Intermittent signaling results directly from the action on inertial forces of chemical distribution. When turbulence acts to fragment a continuous stream of chemicals released from an odor source, patches of ambient fluid are interposed between patches of odor (Murlis and Jones, 1981; Moore and Atema, 1991; Murlis *et al.*, 1992). From the perspective of a sensor in the plume, the patches of chemical in space are detected as pulses in time. The problem of tracking odors to their source is thus a temporal one, requiring the use of a time series of encounters with patches of odor for guidance to their source.

The temporal or spatial dispersal patterns produced by different Reynolds regimes are diverse. However, the Reynolds number points to a principle of similarity as well

as diversity. Regardless of the specific length scale, viscosity, or velocity, conditions with  $Re$  within an order of magnitude are “dynamically similar.” Put another way, any strategy that can lead an agent to the source of a chemical or odor at one combination of viscosity, velocity, and length scale is predicted to work for all combinations of these three variables that have similar Reynolds regimes.

A dramatic demonstration of this principle was the huge smoke plume generated by the recent fire at Los Alamos. Imaged from an orbiting remote sensing platform, the plume from the fire spread eastward over the Rocky Mountains and covered six states. The overall shape was reminiscent of many other plumes (Fig. 1). My colleagues and I could pick out features and characteristic structures that could as easily have been found in a plume from a campfire, in a bathtub, or in one of our laboratory flumes. It is not clear at this time whether animals can recognize the Reynolds regime in which they find themselves and adjust their behavior appropriately; indeed, the problem may be ill-posed. Yet, if this is possible it would be a powerful means

for selection of appropriate strategies by biological or human fabricated autonomous agents.

### Invertebrates and Chemical Plume-Tracking

#### *Plume-tracking behavior*

G. S. Fraenkel and D. L. Gunn defined a set of theoretical mechanisms and proposed that these could explain the orientation behavior of animals (Fraenkel and Gunn, 1961). The *kineses* are defined as undirected reactions to a stimulus: The animal may change direction or speed, systematically or randomly, to the cue or source, but this does not lead to systematic orientation of the animal's body. Kineses are characteristic of bacteria (Berg and Purcell, 1977; Alder, 1987). *Taxes* involve directed reactions to a stimulus. In *klinotaxis* the animal takes sequential samples of a stimulus and estimates whether movement is with or against the spatial gradient of stimulus intensity. Insect maggots and *Euglena* are examples of creatures that use this mechanism (Mast, 1938). *Tropotaxis* is a mechanism by which the animal makes simultaneous comparisons with two or more sensors to yield an instantaneous estimate for guidance to move with or against a cue gradient. The use of two or more spatially separated sensors by odor-tracking decapod crustaceans (Reeder and Ache, 1980; Devine and Atema, 1982; Beglane *et al.*, 1997) and by adult flying insects (Srinivasan *et al.*, 1996, 2001) and walking insects (McCoy, 1984; Bell, 1986) has been interpreted as indicative of a tropotactic mechanism. These theories, already advanced in the 1940s, have had a long and productive influence on ideas of chemo-orientation in animals since. There is a growing understanding, however, that their intuitive appeal often exceeds their practical utility as explanations of specific tracking behavior in turbulent plumes.

Since the pioneering work of J. Murlis (Murlis and Jones, 1981), biologists have been aware of the problems posed by the intermittency caused by the natural odor dispersal and have proposed alternative mechanisms to single modality taxes and kineses. *Odor gated rheotaxis* (OGR) (Kennedy, 1986) combines the guidance provided by two sensory modalities. Thus, while the animal is sensing odor, it moves "upstream" against the ambient fluid flow. When contact with the odor is lost, the motion is directed cross-stream, perpendicular to the mean flow. This "casting," if in the correct direction, can recover contact with the plume and cause a new upstream surge. This mechanism is common among invertebrates; it is found in many species of moths (Kennedy, 1986; Baker *et al.*, 1988; Vickers and Baker, 1992; Mafra-Neto and Carde, 1994; Mafra-Neto and Carde, 1996) and in blue crabs (Weissburg and Zimmer-Faust, 1994; Zimmer-Faust *et al.*, 1995). In recognition of the costs associated with the degree of persistence involved in casting and surging upstream, a variant of OGR called *counterturner*, which incorporates an internal oscillator, has also

been advanced (Belanger and Willis, 1996). Atema has proposed *eddy-chemo-rheotaxis* (ECR) (Atema, 1996), a mechanism in which the microflow-associated eddies produced by turbulence (as contrasted with the mean flow used in OGR) are combined with the "flavor" of the eddy to provide guidance for movement. Eddies dissipate into the ambient flow (have births and deaths) as they move from the source. Thus, depending on the distance from the source at which the animal encounters them, they will possess different characteristics. This is a potentially rich source of information about the nature of the source and its distance from the agent. Speculations about other sources of information for guidance have also been advanced (Grasso *et al.*, 1996a).

As studies of chemo-orientation break away from the classical notions of taxes and kineses, work on OGR and ECR points to two major themes for the future. First is multi-modal research: that information from multiple sensory modalities must inform investigations of olfactory searching behavior. The second theme is the exploitation by searching agents of the structures produced by turbulence as it carries the odor from the source. Further research in these new areas is likely to find many other novel—and to judge from the data provided by animal studies—much more efficient strategies.

*Switching between behaviors.* Animals alter their behavior as they progress through a plume. In the course of a successful tracking episode an animal may show variations in speed or direction that are characteristic of a specific phase of tracking behavior. Lobsters show an initial increase in speed, followed by a steady speed phase, and a final decrease, as they progress toward the source (Moore *et al.*, 1991; Basil, 1994). Their headings also show systematic variation as they track certain types of plumes. Such shifts may be attributed to differences in the spatial organization of the plume (Grasso *et al.*, 1996b). As blue crabs and lobsters near the source, they shift from using their antennules, which are elevated above the substrate, to using the chemo-receptors on their dactyls (feet), which are in contact with the substrate (Moore *et al.*, 1991; Basil, 1994; Weissburg and Zimmer-Faust, 1994).

These behavioral observations, and the changes in the structure of the plume as it evolves on its way downstream, suggest that a critical problem in the design of artificial autonomous systems will be the need to match the tracking algorithm to the ambient conditions. To do this, the robot, like an animal, must be able to recognize a given condition, and particularly those conditions that require a change from one strategy to another. Solutions to the problem may entail (1) shifting modalities; (2) giving a different weight to the information coming from one sensory modality relative to another; or (3) identifying more subtle shifts in the information extracted by a given modality.

### *The spatial biomechanics of olfactory sampling*

The use and integration of multiple sensors is a faculty at which invertebrates seem to excel. Invertebrates bristle with a diversity of chemosensors and fluid-mechanosensors. Indeed, this and similar observations have led some to speculate that invertebrates have pushed their neural processing peripherally to lighten the central processing load and thereby to increase response speed (Wehner, 1987). The preceding discussion of turbulent fluid dispersal underscores the complexity of the problems that animals face in placing and maintaining these sensor arrays in contact with a plume (Fig. 1, inset). To maintain that contact, many invertebrates have evolved modes of body locomotion that are expressed during searching. In particular, the sensors are moved through space (a principle they share with vertebrates) and moveable antennae that place some of the sensors away from the body occur (structures that are atypical of the vertebrate bauplan; though catfish, sea robins, *etc.*, possess chemical sensors at the ends of moveable appendages).

Antennae make the experience of odors very different from our own. Humans, and vertebrates in general, have internal nasal passages that homogenize and obliterate the natural spatial and temporal structure of odor signals before they contact the chemoreceptor. Invertebrates with chemical sensors on the ends of long thin stalks (arthropods, cephalopods, and certain gastropods being common examples) have more direct access to the temporal structure of odor signals produced by turbulence. Distal placement frees the sensors from the boundary layers and hydrodynamic shadow of the body, and movement of the appendages enables a search for contact with the plume in ways that are informed by recent experience. The motions of the whole body are also critical to determining the patterns of spatial sampling experienced by the receptor surface. To the extent that motions of an animal's body and sensory antennae may be important components of any active searching plume-tracking strategy, similar mechanisms would be of great importance in developing autonomous plume-tracking systems.

### *Neural processing of olfactory signals*

That chemoreceptors reside on the ends of antennae, free from body boundary layers, is not evidence that invertebrates actually utilize data about the structure of the odor plume. The chemoreceptors must be fast enough, and sensitive enough, to capture the information and transfer it centrally. Recordings from peripheral chemoreceptors in lobsters (Gomez and Atema, 1996a; Gomez and Atema, 1996b; Gomez *et al.*, 1999) and cockroaches (Lemon and Getz, 1996, 1999) suggest that, to a first approximation, this is the case in both terrestrial and marine invertebrates. Modeling studies of both species, constrained by physio-

logical data, indicate that dynamic information on the time scale of ambient turbulence can be passed centrally and is not filtered out by the chemoreceptors (Getz, 1999; Grasso, unpubl. data).

We know very little about how the natural dynamics of odor signals are processed centrally. Arthropod brains, like those of vertebrates, contain olfactory information-processing centers that are subdivided into glomeruli (Hildebrand and Shepherd, 1997; Derby and Steullet, 2001). These dense regions of neuropile are thought to be the sites of convergence for information about the quality or identity of an odor. Recent research (particularly that employing molecular techniques) has mapped the pathways that carry olfactory information to the glomeruli, and the results support the long-held notion that the coding of odor quality is somehow mirrored in the spatial arrangement of glomeruli (Hildebrand and Shepherd, 1997). A recent study in the three-toed box turtle suggests that concentration coding is independent of this level of anatomical organization in the olfactory bulb (Wachowiak *et al.*, 2000). Variation in odor concentration rather than information about odor quality is the stimulus dimension along which natural odor dynamics information is expected to be encoded in the central nervous system.

The central processing and representation of the dynamics of natural odor has received virtually no attention. Once an animal has solved the quality problem (*i.e.*, an odor has been recognized as worth tracking), information reflecting the temporal series of odor patch encounters must be received, interpreted, and translated into motor commands that lead to the source. An explanation of any piece of this process will aid our understanding of olfactory systems and not just plume tracking. The speed and efficiency with which certain invertebrates (notably arthropods) track a turbulent plume to its source demonstrates that the requisite temporal to spatial transformation can be carried out by the nervous system.

### **Autonomous Systems and Chemical Tracking**

Many simulation studies of chemo-orientation behavior by man-made systems have confirmed that the classic taxes and kineses proposed by Fraenkel and Gunn (1961) can lead to localization of a source in a gradient and have quantitatively delineated the conditions under which taxes and kineses will succeed or fail (Rohlf and Davenport, 1969; Braitenberg, 1984; Beer *et al.*, 1991; Holland and Melhuish, 1996; Ferree *et al.*, 1997). A small number of laboratory robot implementations (Deveza *et al.*, 1994; Ishida *et al.*, 1996; Grasso *et al.*, 2000; Ishida *et al.*, 2001) designed to explain animal chemo-orientation behavior or to produce practical chemical tracking devices have explicitly or implicitly employed various single-modality taxes and kineses. The robot performance, however, has lagged far

behind the expectations raised by successful simulations. The paths taken by robots that have successfully tracked a turbulent plume are very inefficient compared to the paths taken by animals under comparable conditions; and the algorithms used have been effective only in limited contexts (*i.e.*, they do not generalize). These performance discrepancies are not due to sloppy hardware or software implementations of the algorithms; they result from the failure of these mechanisms to account for the realistic fluid dynamics the robots encounter. The gradients present in naively simulated plumes (and tacitly assumed by the single-modality kinesis and taxes by Fraenkel and Gunn) are absent from physical settings where turbulence dominates the patterns of odor dispersal at reasonable time-scales (Warhaft, 2000). The problem rests with our understanding and representation of the environment in simulation studies. The solution requires algorithms that are designed to operate in real plumes rather than smooth gradients.

Improved simulations of real environmental conditions is not a straightforward matter. Simulation of fluid dynamics, with sufficient accuracy, over the required range of temporal and spatial scales is not computationally feasible and perhaps impossible (Warhaft, 2000). An alternative is to capture the dispersal of a given plume in digital form and to use the resulting "digital movie" as the simulation environment. This method is achieved in practice by putting a fluorescent dye into the plume source and capturing the laser-induced fluorescence (LIF) of the dye with digital imaging techniques. From the digital movies, flow fields can simultaneously be obtained for the same plume (Cowen and Monismith, 1997). This "one plume at a time" approach does not lead to generality, but it does allow for the evaluation of many candidate plume-tracking algorithms and for exploring the parameter sensitivity of those algorithms under realistic fluid conditions. This simulation prescreening can be done on a scale that would be impracticable with robots.

These LIF methods, however, cannot include the agent's own influence on turbulent dispersal as it moves through the plume. For this, and to avoid the false sense of progress described in the first paragraph in this section, robots must provide the final test. Robotic studies of chemical plume tracking progress more slowly from simulation studies (but faster than animal studies!). Therefore, a combination of prescreening of algorithms in simulation to weed out patently unsuccessful strategies, followed by definitive testing with robots seems a sound approach.

Compared to the toy problems with which robots and experimental animals are challenged in the laboratory (where experimental control requires variables to be held to a minimum), resource localization problems in natural settings are vastly more complex at many levels. Physical hazards, obstacles, competitors, and predators require behavioral responses that interrupt the smooth application of a foraging strategy. The recognition of false cues, early aban-

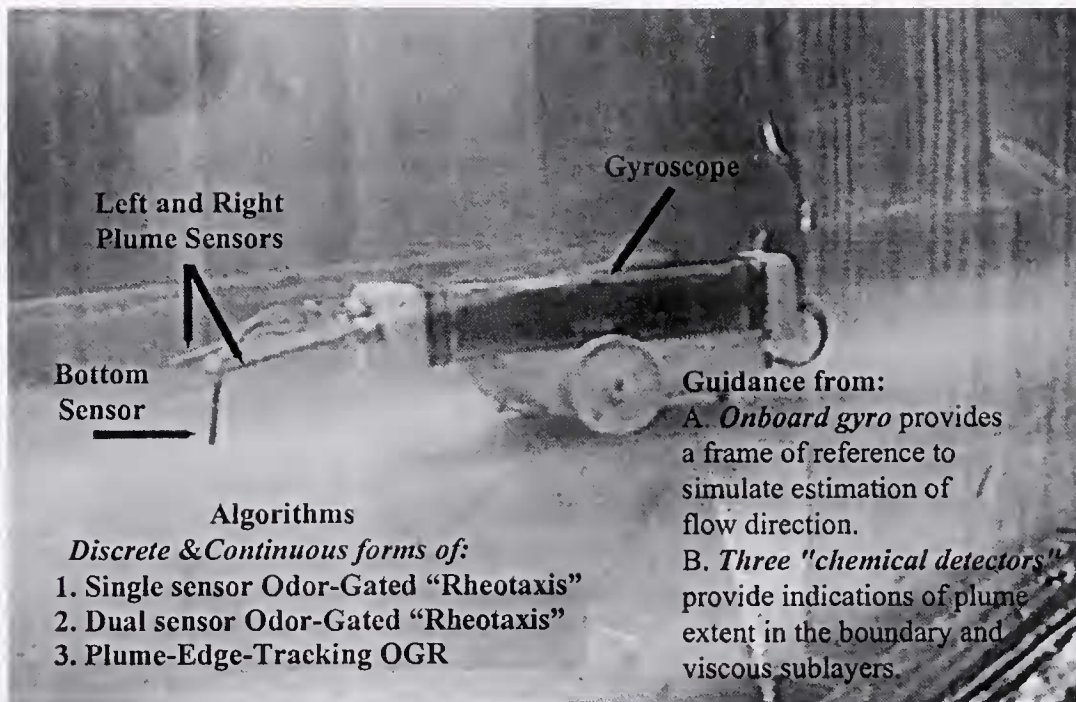
donment of false trails, and maintenance of a stream of appropriate guidance information in unpredictable environments may also require real-world animals and robots to employ a hierarchy of behavioral responses that may deviate from the application of a single simple mechanism. A mechanism that switches between strategies when conditions change, or that varies the weighting of sensory modalities with their reliability, offers solutions to many of these difficulties. Such strategies—so essential for the success of autonomous systems—have scarcely been addressed in animal and biomimetic robotic studies.

### Biomimetic Robots and Hypothesis Testing Methods

The preceding sections show that fluid mechanics, animal behavior, neuroscience, and cybernetics can each contribute to the understanding that will finally permit us to construct autonomous systems that can locate resources based on their chemical signature and under chaotic environmental conditions. Each field has reached a point where its methodology has provided tantalizing hints about the robust plume-tracking strategies of invertebrates; but each faces difficult technical and conceptual hurdles before it can advance further. Biomimetic robots offer a methodology that can answer some of the questions raised by each of these approaches.

In my own studies, conducted with colleagues in the laboratory of J. Atema at the Marine Biological Laboratory in Woods Hole, the behavior of a robot told us something unsuspected about the plume structure (Grasso *et al.*, 1996b). The behavior of this robot changed in different regions of the plume as it was executing a simple tropotactic tracking algorithm. This result indicated a qualitative difference in plume structure from the robot's perspective and serves notice that changes in animal behavior must be interpreted with caution. We have also explored spatial sampling issues by varying the separation between paired sensors (Grasso *et al.*, 1997). This work had an engineering aspect—finding an optimal sampling configuration—and a biological aspect—determining the information that animals obtain from the inter-sensor separations they possess. We have also studied tropotactic algorithms in one (jet) plume (Grasso *et al.*, 2000) and OGR in two (leaky) plumes (Grasso, unpubl. data) that American lobsters are known to track. As these robot experiments accumulate, they raise new biological questions and narrow the possible biological and physical explanations of plume tracking by lobsters.

The performance of the robots used in these studies was *quantitatively* evaluated against the performance of the American lobster. This unique comparison was possible because we tested the robot under physical conditions virtually identical to those under which animal experiments had previously been conducted (*i.e.*, the plume was composed of a natural food extract for the lobster and a synthetic tracer for the robot, but all other experimental conditions



**Figure 2.** One of our biomimetic robots, in the large flume facility at the Marine Biological Laboratory, Woods Hole. The biologically inspired chemical sensing aquatic autonomous robots (BISAAR) are equipped with two antenna-like fluorescence sensors that detect fluorescein dye with the spatial (1 mm) and temporal ( $>5$  Hz) resolution of the lobster lateral antennule. From this information, and an approximation of the mean flow in the tank provided by a gyroscope, the BISAAR robots are a platform for exploring plume-tracking algorithms. The third chemical sensor, the "bottom sensor," pointed toward the flume floor is intended to fulfill part of the role of the chemical sensors on the legs of real lobsters. It is used in studies of behavioral switching between antennule and leg-guided chemo-orientation. The wheeled chassis is capable of propelling and turning faster than its biological counterparts, so to a first approximation it achieves locomotory biomimetic scaling.

were identical). The comparison was also possible because the critical factors of robot hardware and software required to implement the algorithms were matched to the corresponding biological characteristics of the lobster (Fig. 2). I refer to this as *biomimetic scaling*.

My use of the term biomimetic is not intended to denote a slavish mimicry of all the biological details. The mimicry is primarily conceptual and is structural only as needed to support the conception. The idea of biomimetic scaling is to reproduce only those points that are essential to test a given hypothesis. Thus, to test the power of OGR or tropotaxis as explanations of plume tracking by lobsters, we constrained the following critical features to known lobster values: body size and shape, sensor arrangement in space, speed and pattern of locomotion, and temporal and spatial resolution of the sensors in the robots' hardware and software to known lobster values (Grasso *et al.*, 2000).

These experiments were conducted to evaluate behavioral theories. The results, while germane to the plume-tracking problem, had broader implications for the study of fluid mechanics, cybernetics, and neuroscience, as noted above. Continued studies with more strenuous constraints—from

implementation of a realistic neural architecture, to software or sensors configured to take advantage of fluid flow around the robot in ways that mimic antennal morphology—will lead to the evaluation of theories with ever-greater explanatory (or exclusionary) power. In future studies, biomimetic scaling will allow us to use robots to explore issues of neural processing and biomechanical strategies of spatial sampling.

Though space prohibits a detailed review, note that affordable technologies are available from commercial suppliers to make small processors and actuators as well as biologically scaled sensors that are suitable to meet the demands of biomimetic scaling (Ishida *et al.*, 2001; Robert, 2001).

## Conclusions

With the methodology described in this paper, we cannot "prove" that the algorithms biomimetic robots implement are the exact analogs of biological mechanisms. Those mechanisms can only be determined from biological experiments. But in the application of the scientific method, we

can exclude untenable biological explanations, simply stating that they fail to account for the biological behavior.

As this process of excluding the biologically implausible proceeds, something unrelated will occur in parallel. The ability of the robots to track chemical plumes to their source will improve as their performance approaches that of real animals. Thus, although there is no scientific guarantee that the robots will ever match their biological models, a realizable benchmark will be systematically approached. The algorithms gleaned from these biologically inspired studies can find practical application as components in autonomous systems intended for exploration.

Though the "one plume at a time" approach is a slow and inductive one, the principle of "dynamic similarity" indicates that strategies developed in one context may find general utility in autonomous systems that are designed to operate at a variety of scales with coincidental Reynolds numbers. This extends to regimes in fluids of different viscosity like water and air (or any fluid for that matter). Studies of behavioral switching by animals may help to demarcate these boundaries and may also suggest control hierarchies that will recognize strategies appropriate to particular fluid-dynamic contexts.

Finally, invertebrates offer excellent models for the study of plume tracking. Their external sensors, borne on movable antennae, provide access to dynamic information associated with plume structures that is simply not available to vertebrates with internal noses. This may mean a richer diversity of information, and by analogy to the significance of eye movements for visual information processing (Yarbus, 1967), the motions of the antennae provide an easily assayed indication of information-processing strategies.

### Acknowledgments

This work was supported in part by a grant from the joint DARPA/ONR plume-tracing program administered by Keith Ward (ONR) and Regina Dugan (DARPA). I thank Jelle Atema, Jennifer Basil, David Mountain, and Rainer Voigt for stimulating and inspiring discussions; Lisa Borden, Todd Cowen, Jonathan Dale, Kevin Dittmer, and John Hanna, for technical assistance; Diana Blazis and Pam Oldham for making the ISIP-BIAS symposium possible and successful; and Todd Cowen, Jeff Kosseff, and Don Webster for discussions of fluid dynamics and for drawing my attention to the Los Alamos plume.

### Literature Cited

- Alder, J. 1969. Chemoreceptors in bacteria. *Science* **166**: 1588–1597.
- Alder, J. 1987. How motile bacteria are attracted and repelled by chemicals: an approach to neurobiology. *Biol. Chem.* **386**: 163–173.
- Atema, J. 1996. Eddy chemotaxis and odor landscapes: exploration of nature with animal sensors. *Biol. Bull.* **191**: 129–138.
- Baker, T. C., B. S. Hansson, C. Lofstedt, and J. Lofqvist. 1988. Adaptation of antennal neurons in moth is associated with cessation of pheromone-mediated upwind flight. *Neurobiology* **85**: 9826–9830.
- Basil, J., and J. Atema. 1994. Lobster orientation in turbulent odor plumes: simultaneous measurement of tracking behavior and temporal odor patterns. *Biol. Bull.* **187**: 272–273.
- Beer, R. D., H. J. Chiel, and L. S. Sterling. 1991. An artificial insect: computer-simulated insects that adapt to their environment may be the next stage in evolution of artificial intelligence. *Am. Sci.* **79**: 444–452.
- Beglane, P. F., F. W. Grasso, J. A. Basil, and J. Atema. 1997. Far field chemo-orientation in the American lobster, *Homarus americanus*: effects of unilateral ablation and lesioning of the lateral antennule. *Biol. Bull.* **193**: 214–215.
- Belanger, J. H., and M. A. Willis. 1996. Adaptive control of odor-guided locomotion: behavioral flexibility as an antidote to environmental unpredictability. *Adapt. Behav.* **4**: 217–253.
- Bell, W. J. 1986. Responses of arthropods to temporal chemical stimulus changes: simulation of a humidity differential and a pheromone plume. Pp. 139–148 in *Mechanisms in Insect Olfaction*, T. L. Payne, M. C. Birch, and C. E. J. Kennedy, eds. Clarendon Press, Oxford.
- Berg, R. C., and E. M. Purcell. 1977. The physics of chemoreception. *Biophysics* **20**: 193–219.
- Braitenberg, V. 1984. *Vehicles: Experiments in Synthetic Psychology*. Bradford Books, MIT Press, Cambridge, MA.
- Cowen, E. A., and S. G. Monismith. 1997. A hybrid digital particle tracking velocimetry technique. *Exp. Fluids* **22**: 199–211.
- Derby, C. D., and P. Steullet. 2001. Why do animals have so many receptors? The role of multiple chemosensors in animal perception. *Biol. Bull.* **200**: 211–215.
- Deveza, R., D. Thiel, A. Russell, and A. Mackay-Sim. 1994. Odor sensing for robot guidance. *Int. J. Robot. Res.* **13**: 232–239.
- Devine, D. V., and J. Atema. 1982. Function of chemoreceptor organs in spatial orientation of the lobster, *Homarus americanus*: differences and overlap. *Biol. Bull.* **163**: 144–153.
- Ferree, T. C., T. M. Morse, and S. R. Lockery. 1997. Neural networks for chemotaxis in *C. elegans*: rule extraction and robotics. Society for Neuroscience: 27th Annual Meeting, New Orleans, 25–30 October 1997. Abstr. #527.10.
- Ford, N. B. 1986. The role of pheromone trails in the sociobiology of snakes. Pp. 261–278 in *Chemical Signals in Vertebrates*, D. Duvall, D. Muller-Schwartz, and R. M. Silverstein, eds. Plenum, New York.
- Ford, N. B., and J. R. Low. 1984. Sex pheromone source location by garter snakes: a mechanism of detection of direction in nonvolatile trails. *J. Chem. Ecol.* **10**: 1193–1199.
- Fraenkel, G. S., and D. L. Gunn. 1961. *The Orientation of Animals: Kineses, Taxes and Compass Reactions*. Dover, New York.
- Getz, W. 1999. A kinetic model of the transient phase in the response of olfactory receptor neurons. *Chem. Senses* **24**: 497–508.
- Gibson, J. J. 1982. Ecological physics, magic and reality. Pp. 217–223 in *Reasons for Realism: Selected Essays of James J. Gibson*, R. Edward and R. Jones, eds. Lawrence Erlbaum Associates, London.
- Gomez, G., and J. Atema. 1996a. Temporal resolution in olfaction: stimulus integration time of lobster chemoreceptor cells. *J. Exp. Biol.* **199**: 1771–1779.
- Gomez, G., and J. Atema. 1996b. Temporal resolution in olfaction II: time course of recovery from adaptation in lobster chemoreceptor cells. *J. Neurophysiol.* **76**: 1340–1343.
- Gomez, G., R. Vnigt, and J. Atema. 1999. Temporal resolution in olfaction III: flicker fusion and concentration-dependent synchronization with stimulus pulse trains of antennular chemoreceptor cells in the American lobster. *J. Comp. Physiol.* **185**: 427–436.
- Grasso, F. W., T. Consi, D. Mountain, and J. Atema. 1996a. Locating odor sources in turbulence with a lobster inspired robot. Pp. 104–112 in *From Animals to Animals 4: Proceedings of the Fourth International Conference on Simulation of Adaptive Behavior*, P. Maes, M. J. Ma-



- taric, J.-A. Meyer, J. Pollack, and S. W. Wilson, eds. MIT Press, Cambridge, MA.
- Grasso, F. W., J. H. Dale, T. R. Consi, D. C. Mountain, and J. Atema. 1996h. Behavior of purely chemotactic robot lobster reveals different odor dispersal patterns in the jet region and the patch field of a turbulent plume. *Biol. Bull.* **191**: 312–313.
- Grasso, F. W., J. H. Dale, T. R. Consi, D. C. Mountain, and J. Atema. 1997. Effectiveness of continuous bilateral sampling for robot chemotaxis in a turbulent odor plume: implications for lobster chemotaxis. *Biol. Bull.* **193**: 215–216.
- Grasso, F. W., T. R. Consi, D. C. Mountain, and J. Atema. 2000. Biomimetic robot lobster performs chemo-orientation in turbulence using a pair of spatially separated sensors: progress and challenges. *Robot. Aut. Sys.* **30**: 115–131.
- Hamner, P., and W. M. Hamner. 1977. Chemosensory tracking of scent trails by the planktonic shrimp *Acetes sibogae australis*. *Science* **195**: 886–888.
- Hildebrand, J. G., and G. M. Shepherd. 1997. Mechanisms of olfactory discrimination: converging evidence for common principles across phyla. *Annu. Rev. Neurosci.* **20**: 595–631.
- Holland, O., and C. Melhuish. 1996. Some adaptive movements of animats with single symmetrical sensors. Pp. 53–64 in *From Animals to Animats: Proceedings of the Fourth International Conference on Simulation of Adaptive Behavior*, P. Maes, M. J. Mataric, J.-A. Meyer, J. Pollack, and S. W. Wilson, eds. MIT Press, Cambridge, MA.
- Ishida, H., Y. Kagawa, T. Nakamoto, and T. Moriizumi. 1996. Odor-source localization in the clean room by an autonomous mobile sensing system. *Sensors and Activators B* **33**: 115–121.
- Ishida, H., T. Nakamoto, T. Moriizumi, T. Kikas, and J. Janata. 2001. Plume-tracing robots: a new application of chemical sensors. *Biol. Bull.* **200**: 222–226.
- Kennedy, J. S. 1986. Some current issues in orientation to odour sources. Pp. 11–25 in *Mechanisms in Insect Olfaction*, T. L. Payne, M. C. Birch, and C. E. J. Kennedy, eds. Clarendon Press, Oxford.
- Lemon, W. C., and W. M. Getz. 1996. Temporal resolution of general odor pulses by olfactory sensory neurons in American cockroaches. *J. Exp. Biol.* **200**: 1809–1819.
- Lemon, W. C., and W. M. Getz. 1999. Responses of cockroach antennal lobe projection neurons to pulsatile olfactory stimuli. *Ann. N. Y. Acad. Sci.* **855**: 517–520.
- Mafra-Neto, A., and R. T. Carde. 1994. Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. *Nature* **369**: 142–144.
- Mafra-Neto, A., and R. T. Carde. 1996. Dissection of the pheromone-modulated flight of moths using single-pulse response as a template. *Experientia* **52**: 373–379.
- Mast, S. O. 1938. Factors involved in the orientation of lower organisms to light. *Biol. Rev.* **13**: 186–224.
- McCoy, M. M. 1984. Antennal movements of the American cockroach *Periplaneta americana*. Ph.D. dissertation, University of Kansas, Lawrence.
- Moore, P. A., and J. Atema. 1991. Spatial information in the three-dimensional fine structure of an aquatic odor plume. *Biol. Bull.* **181**: 408–418.
- Moore, P. A., N. Scholz, and J. Atema. 1991. Chemical orientation of lobsters, *Homarus americanus*, in turbulent odor plumes. *J. Chem. Ecol.* **17**: 1293–1307.
- Morse, T. M., T. C. Ferree, and S. R. Lockery. 1998. Robust spatial navigation in a robot inspired by chemotaxis in *Caenorhabditis elegans*. *Adapt. Behav.* **6**: 393–410.
- Mountain, D. C., and A. E. Hubbard. 2001. Sensing scenes with silicon. *Biol. Bull.* **200**: 227–234.
- Murlis, J., and C. D. Jones. 1981. Fine-scale structure of odour plumes in relation to insect orientation to distant pheromones and other attractant sources. *Physiol. Entomol.* **6**: 71–86.
- Murlis, J., J. S. Elkinton, and R. T. Carde. 1992. Odor plumes and how insects use them. *Annu. Rev. Entomol.* **37**: 505–532.
- Pierce-Shimomura, J. T., T. M. Morse, and S. R. Lockery. 1999. The fundamental role of pirouettes in *Caenorhabditis elegans* chemotaxis. *J. Neurosci.* **19**: 9557–9569.
- Reeder, P. B., and B. W. Ache. 1980. Chemotaxis in the Florida spiny lobster, *Panulirus argus*. *Anim. Behav.* **28**: 831–839.
- Robert, D. 2001. Innovative biomechanics for directional hearing in small flies. *Biol. Bull.* **200**: 190–194.
- Rohlf, J. F., and D. Davenport. 1969. Simulation of simple models of animal behavior. *J. Theor. Biol.* **23**: 400–424.
- Snyder, N. F. R., and H. A. Snyder. 1971. Pheromone-mediated behaviour of *Fasciolaria tulipa*. *Anim. Behav.* **19**: 257–268.
- Srinivasan, M. V., S. Zhang, and J. S. Chahl. 2001. Landing strategies in honeybees and possible applications to autonomous airborne vehicles. *Biol. Bull.* **200**: 216–221.
- Srinivasan, M. V., S. W. Zhang, M. Lehrer, and T. S. Collett. 1996. Honeybee navigation en route to the goal: visual flight control and odometry. *J. Exp. Biol.* **199**: 237–244.
- Vickers, N. J., and T. C. Baker. 1992. Male *Heliothis virescens* maintain upwind flight in response to experimentally pulsed filaments of their sex pheromone (Lepidoptera: Noctuidae). *J. Insect Behav.* **5**: 669–687.
- Wachowiak, M., M. Zochowski, L. B. Cohen, and C. X. Falk. 2000. The spatial representation of odors by olfactory receptor neuron input to the olfactory bulb is concentration invariant. *Biol. Bull.* **199**: 162–163.
- Warhaft, Z. 2000. Passive scalars in turbulent flows. *Annu. Rev. Fluid Mech.* **32**: 203–240.
- Wehner, R. 1987. Matched filters—neural models of the external world. *J. Comp. Physiol. A* **161**: 511–531.
- Weissburg, M. J., and R. K. Zimmer-Faust. 1994. Odor plumes and how blue crabs use them in finding prey. *J. Exp. Biol.* **197**: 349–375.
- Wells, M. J., and S. K. L. Buckley. 1972. Snails and trails. *Anim. Behav.* **20**: 345–355.
- Wilson, E. O. 1962. Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 1. The organization of mass foraging. *Anim. Behav.* **10**: 134–147.
- Yarbus, A. L. 1967. *Eye Movements and Vision*. Plenum Press, New York.
- Yen, J. 2000. Life in transition: balancing inertial and viscous forces by planktonic copepods. *Biol. Bull.* **198**: 213–224.
- Zimmer-Faust, R. K., C. M. Finelli, N. D. Pentcheff, and D. S. Wetthey. 1995. Odor plumes and animal navigation in turbulent water flow: a field study. *Biol. Bull.* **188**: 111–116.